Neural Correlate of Perceptual Adaptation to Gratings

Abstract. *Exposure of simple cells of the cat striate cortex to high-contrast drifting gratings greatly reduces the subsequent response of the cells to low-contrast gratings. This adaptation effect has an average duration of 30 seconds and shows interocular transfer and selectivity for spatial frequency and orientation. This effect is strikingly similar to the perceptual adaptation to high-contrast gratings.*

Blakemore and Campbell (*1*) showed that prolonged observation of a grating of high contrast greatly reduces the visibility of a low-contrast grating of the same spatial frequency. One can experience this effect by inspecting the upper left grating of Fig. 1 for about 1 minute. After this adaptation period the central grating can hardly be detected.

This effect should not be mistaken for the well-known phenomenon of light and dark adaptation. The gratings in Fig. 1 have the same average luminance and differ only in contrast. This phenomenon is highly selective for orientation and spatial frequency: The visibility of a grating of low contrast is not affected by adaptation to gratings of different orientation or spatial frequency (*1*).

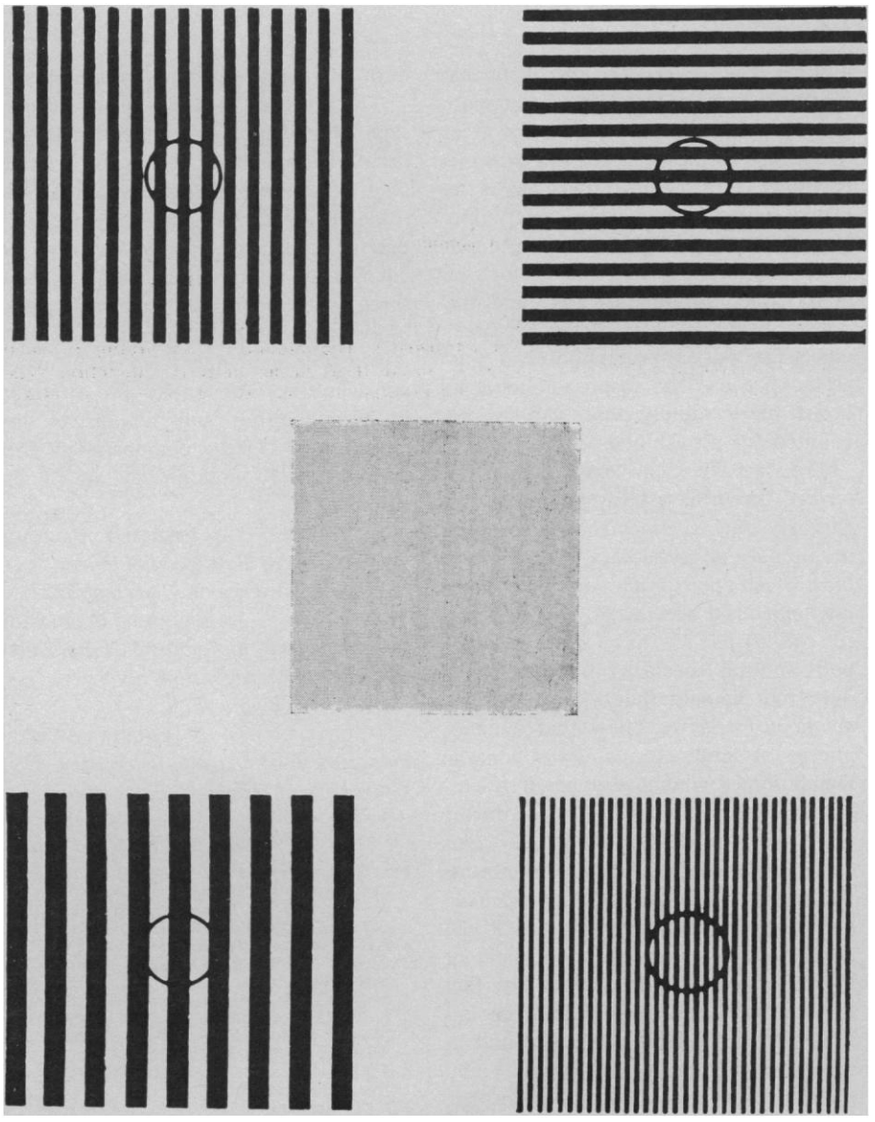

Fig. 1. Perceptual adaptation to gratings. The grating at upper left and the central grating have the same spatial frequency, but the latter has lower contrast. If one looks at the upper left grating for about 1 minute with gaze moving around the small circle and then looks at the low-contrast grating, the latter grating seems invisible for a few seconds. Looking at the horizontal grating or at a vertical grating of different spatial frequency has no effect on the visibility of the central grating. [Modified from Blakemore and Campbell (*1*)]

In this report we present evidence that the simple cells of the cat striate cortex exhibit adaptation to gratings with properties similar to the perceptual adaptation observed in man. Twenty cats were studied. Under halothane anesthesia, an endotracheal tube and a venous cannula were inserted. A plastic chamber was positioned around a small opening of the skull overlying area 17 of the cortex and fixed firmly to the skull with dental cement. After removal of the dura, anesthesia was terminated and the cat was immobilized with curare and artificially ventilated with room air.

The animal was fixed to the recording table by bolting the rim of the plastic chamber to a suitable metal mounting. The pupils were dilated with atropine, and contact lenses with artificial pupils of 4-mm diameter were applied to both eyes. Refraction was corrected with additional lenses.

Action potentials from visual cortical neurons were recorded with tungsten microelectrodes. For each cell, the receptive fields of both eyes were mapped on a tangent screen. Then the screen of an oscilloscope was centered with respect to the receptive field of one eye, and the other eye was covered. A drifting sinusoidal grating of suitable orientation, spatial frequency, and contrast was generated on the face of the oscilloscope. The rate of discharge of the cell was counted every second.

We recorded from 101 units with receptive fields within 5° of the area centralis. Of these units, 55 were classified as "simple," 30 as "complex," 5 as "hypercomplex," and 11 as geniculate fibers. Particular attention was devoted to the distinguishing between simple and complex cells by the criteria of Hubel and Wiesel (*2*) and Pettigrew *et al.* (*3*). In addition, we took into account the different responses of simple and complex cells to drifting gratings (*4*).

After the cell receptive field was mapped, the grating was oriented parallel to the preferred orientation of the cell and moved at constant velocity in the preferred direction. The responses to drifting gratings of various spatial

frequencies were assessed by listening to the unit discharge amplified via a loudspeaker, and the frequency was chosen which gave the lowest contrast threshold. The contrast of the grating was then set at a value three times the threshold, and the average rate of discharge in response to this test stimulus was recorded for a minute. Then the contrast was set at the highest available value (60 percent) (*5*), and the cell was exposed to this stimulus (adapting stimulus) for 1 minute. Last, the contrast was lowered to its initial value, and the response to the test stimulus was recorded for at least 1 minute.

Figure 2 illustrates the adaptation of a simple cell. The nerve impulses were recorded on a penwriter that displays an integration of the number of nerve impulses per second. The top record shows the response to a drifting grating of relatively low contrast (the test stimulus), and then the response to the adapting grating of high contrast. The bottom record shows the end of the adaptation period and the subsequent slow recovery of the response to the test grating. In this case, the response to the test stimulus returned to its initial value in about 30 seconds. For all other simple cells examined, the recovery time after 1 minute of adaptation varied from 20 seconds to about 2 minutes. The complex cells seemed to fall into two classes: The first class showed no appreciable adaptation effect, and the second had an adaptation effect of, at most, 10 to 15 seconds.

Two kinds of evidence demonstrate that the adaptation effect is not due to fatigue of the cell under the high-contrast stimulation. First, the response to the high-contrast grating remains practically stationary after an initial transient (Figs. 2 and 3). Second, in another series of experiments we found that the cells adapt even when part of the cell receptive field (central region) is masked so that cell response to the adapting grating is abolished or reduced to a discharge rate lower than the test response. Possible interpretations of this second series of experiments is that some input cell has adapted or that the exposure of only a particular part of the receptive field is sufficient to cause adaptation; the data do not permit definite conclusions.

The average duration of adaptation of the 55 simple cells was about 30 seconds, of the same order as that for perceptual adaptation in man. Moreover, as mentioned for perceptual adaptation, the simple cell adaptation is also selective for orientation and spatial frequency: There is no adaptation when the orientation or the spatial frequency of the high-contrast grating falls outside the orientation or spatial frequency channel of the cell.

The adaptation in simple cells of the cortex is mostly of cortical origin, since it shows interocular transfer (Fig. 3). A clear adaptation effect was found both when the right eye was adapted and the left eye was tested (Fig. 3, left) and when the situation was reversed (Fig. 3, right). This is a further similarity to perceptual adaptation to gratings, which also shows binocular transfer (*1*). Additional evidence that the effect of adaptation is mostly cortical comes from the observation that the geniculate fibers used for recording showed either no adaptation or an effect as short as 2 to 3 seconds.

The present results suggest that perceptual adaptation to gratings is the outcome of neural phenomena of adaptation such as the ones we observed in the simple cells of the cat striate cortex. These results also seem relevant to the problem of hierarchical organization of cortical cells. Hubel and Wiesel (*2*) proposed a model in which complex cells would be built up from the convergence of several simple cells (*2*).

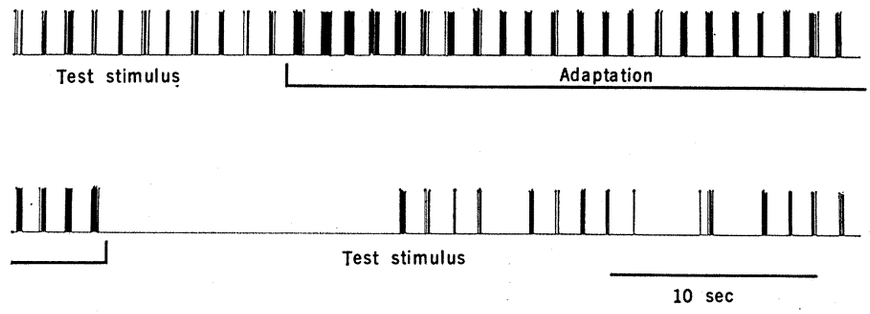

Fig. 2. Adaptation of a simple cell to a grating. The spike activity of a simple cell of the striate cortex was recorded on a penwriter. The stimulus was a grating oriented at the preferred orientation of the cell and drifting in its preferred direction. The average luminance of the grating was kept constant at 2 cd/m^2. The clusters of spikes in the record are the responses of the cell to a single period of the grating. In the first and last parts of the record (test stimulus), the contrast was 6 percent, three times the threshold. During the 1-minute period of adaptation (time span shown by heavy line beneath record), the contrast was raised to about 55 percent. After the adaptation period, the cell did not respond at all to the test stimulus for 14 seconds and slowly recovered in another 15 seconds.

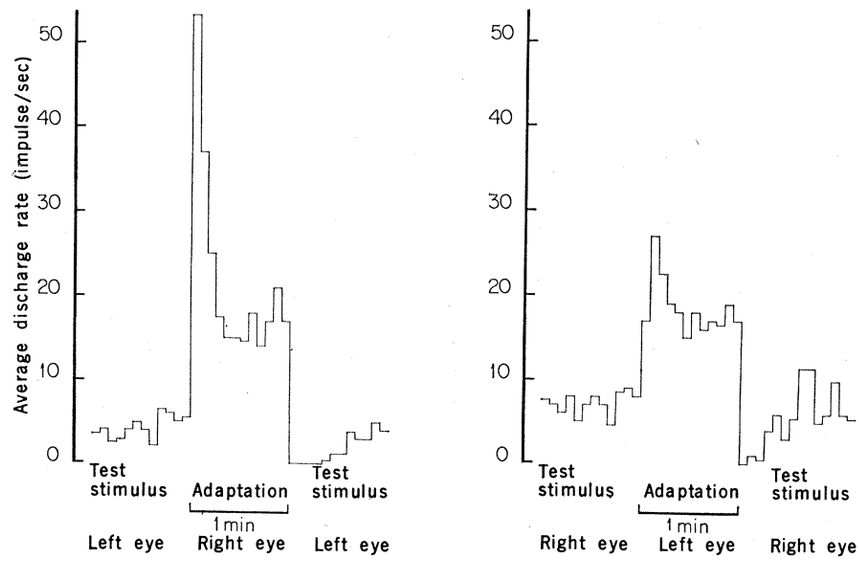

Fig. 3. Interocular transfer of adaptation in a simple cell. The tracings are continuous records of the discharge rate of the cell averaged for 5-second intervals before, during, and after adaptation. In the record at left, the cell was adapted by exposing the right eye to the high-contrast grating and tested before and after adaptation by exposing the left eye to the low-contrast grating. The conditions were reversed in the right record.

The fact that complex cells either do not adapt or, if they do adapt, recover much faster than simple cells is not easy to reconcile with Hubel and Wiesel's hypothesis.

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References and Notes

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3. J. D. Pettigrew, T. Nikara, P. O. Bishop, *Exp. Brain Res.* **6**, 373 (1968).
4. L. Maffei and A. Fiorentini, *Vision Res.* **13**, 1255 (1973).
5. The contrast C of the grating is defined as $C = (L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min} are the luminances of the bright and dark bars, respectively.

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Stimulus Change Contemporaneous with Food Presentation Maintains Responding in the Presence of Free Food

Abstract. *The presence or absence of a change in the ambient stimulus conditions upon entry into a food source controlled the frequency with which pigeons choose one of two concurrently available grain sources. Such changes characteristically accompany the production of response-produced food and account for prior reports of responding to produce food in the presence of freely available food.*

Several experiments (*1–4*) demonstrate that rats and pigeons acquire and continue to emit food-producing responses in the presence of freely available food. For example, Neuringer (*3*) showed that experimentally naive pigeons would acquire a new food-producing response in the presence of freely available food. Since many theories of learning assume that deprivation is a necessary antecedent of performance (*5*), these results are of substantial interest.

The two experiments presented here show that responding in the presence of free food need not be attributed to the "intrinsic appeal" of food-producing responses (*2*) nor does the "act of producing food" appear to have any special motivational properties (*3*). Rather, responding in the presence of free food is maintained by the externally produced stimulus change which characteristically accompanies the presentation of response-produced food but which does not typically occur during the consumption of free food.

In experiment 1, two White Carneaux pigeons (1411 and 2769) with varied experimental histories were placed in a chamber 38 cm high, 31 cm wide, and 31 cm long. Prior to the experiment both pigeons were allowed to feed freely in their home cages for several days. The chamber contained a response disk (1.9 cm in diameter), a Gerbrands food hopper mounted on one wall, and a filled food cup mounted on the opposite wall. Water and grit were freely available at all times. A photocell and its light source were mounted over the free-food cup (*6*). For the first six 24-hour sessions a single peck to the illuminated response disk allowed the pigeon to eat grain from the hopper for 3 seconds; the bird could also eat from the free-food cup. Pecks to the disk illuminated the grain hopper, turned off the light which illuminated the response disk, turned out the house light which provided general illumination to the chamber, and produced the grain hopper with an audible click. Entries into the free-food cup produced no stimulus change. For the next six sessions, pecks to the response disk produced access to the grain hopper but no other changes in the ambient stimulus conditions (the grain hopper remained continuously illuminated). Entries into the free-food cup turned on a light over the free-food cup, turned the house light off, and produced an audible click by a solenoid behind the free-food cup. For the last six sessions (12 sessions for pigeon 1411), the original conditions were reinstated.

The number of pecks made to the response disk during each session of the three conditions is presented in Fig. 1. Responding was maintained in the first and last conditions when pecks produced both food and stimulus change. However, responding was not maintained when pecks produced only food and entries into the free-food cup provided food and stimulus change.

In experiment 2, the effect of stimulus change associated with one of two free-food sources was studied. Four experimentally naive White Carneaux pigeons (B-17, B-18, B-19, and B-20) were employed. Each pigeon was placed in a chamber 27.5 cm high, 25.0 cm wide, and 30.0 cm long. Rectangular openings on opposite side walls permitted access to the two free-food cups. Throughout the experiment, grain was only available during the experimental sessions and water and grit were only available in the home cage. During the first experimental condition the right food cup was constantly illuminated. Entries into the right food cup produced no stimulus change. Entries into the left food cup turned on a light over the cup, turned off the house light, and produced an audible click by a solenoid. This condition was in effect for a minimum of 20 1.5-hour sessions and until five consecutive sessions occurred with no apparent directional trend. A limit of 50 sessions was set for any case in which stability was not achieved in fewer sessions. After stability was achieved, the conditions were reversed. This condition was also in effect until the criteria described

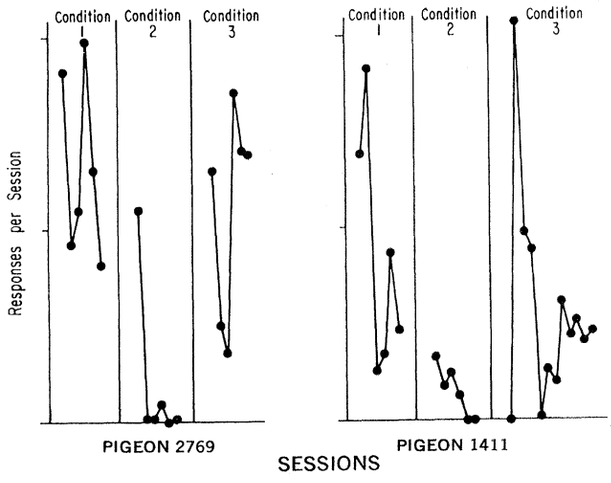

Fig. 1. Responses per 24-hour session for two White Carneaux pigeons (1411 and 2769). In conditions 1 and 3, responses produced food plus stimulus change. In condition 2, responses produced only food and entries into the free-food cup produced stimulus change.